Nebraskophis HOLMAN from the Late Eocene of Georgia (USA), the oldest known North American colubrid snake

Dennis PARMLEY and J. Alan HOLMAN

Abstract. An extinct colubrid snake of the genus *Nebraskophis* is reported on the basis of a trunk vertebra from the Late Eocene (36.0-34.2 Ma) of central Georgia, USA. The fossil represents the oldest record of the family Colubridae in North America, and is equivalent to, or slightly older in age than the previously oldest known colubrid remains from the Late Eocene of Thailand. The age and remarkable similarity of the fossil to living colubrid vertebrae suggest that the origin of colubrid snakes considerably predates the Late Eocene. The presence of *Nebraskophis* in Georgia supports the hypothesis of an early Cenozoic biogeographic connection between the Great Plains and southeastern region of the United States for at least some early colubrids. The genus probably evolved autochthonously on the continent rather than arriving as a Eurasian immigrant.

Key words: *Nebraskophis.* Late Eocene, Georgia, USA, oldest North American colubrid snake.

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I. INTRODUCTION

With the exception of palaeopheids (PARMLEY and CASE 1988; HOLMAN 2000), fossil snakes from the Eocene of North America are uncommon. Our present knowledge of North American Eocene snakes consists of aniliid and boid species and two genera of palaeopheids (HOLMAN 2000). The Late Eocene snake fauna of North America is especially depauperate with only two small terrestrial erycine boids (*Calamagras weigeli* HOLMAN and *Ogmophis compactus* LAMBE) and one palaeopheid species (*Pterosphenus schucherti* LUCAS; HOLMAN 2000). Here, a relatively well preserved colubrid vertebra of the extinct genus *Nebraskophis* is reported from the Late Eocene (Chadronian Land Mammal Age) Hardie Mine local fauna (hereafter l.f.) of Wilkinson County, central Georgia, USA. Prior to the discovery of the Hardie Mine colubrid, the oldest known colubrid snakes were from the Late Eocene of Thailand (six generically indeterminate vertebrae; RAGE et al., 1992) and the early Oligocene of North America (*Floridaophis auffenbergi* HOLMAN; *Nebraskophis oligocenicus* HOLMAN; *Texasophis galbreathi* HOLMAN; HOLMAN 1999, 2000), Europe (*Colu-*

ber cadurci RAGE; RAGE 1988), and Asia (reported as indeterminate Colubridae; THOMAS et al., 1991) Thus, the Hardie Mine fossil is important because (1) it represents the earliest record of the family Colubridae in North America and (2) it sheds new information on the evolution and origin of early archaic colubrid snakes in general.

    T h e H a r d i e M i n e l o c a l i t y. The Hardie Mine site is an inactive open-pit kaolin mine located 3.9 km NNW of Gordon (32° 54.335'N, 83° 21.543'W latitude and longitude), Wilkinson County, central Georgia (Fig. 1). An approximately one meter thick stratum of *in situ* fossiliferous Clinchfield Formation sediments (basal unit of the Barnwell Group; HUDDLESTUN and HETRICK, 1985) is exposed in the north wall of the mine. Recent screen washing and sorting of approximately 250 kg of these sediments by Georgia College & State University parties has yielded numerous microfossils of shark teeth, ray oral teeth, tiny bony fish teeth and otoliths, a few small palaeopheid snake vertebrae, and the colubrid snake vertebra reported here. While most of the Hardie Mine fossils remain undescribed, WESTGATE (2001) recently published a discussion on paleoecological aspects of the Hardie Mine l.f. and a list of the vertebrates he identified from the site. It is important to note that the *in situ* Clinchfield sediments that yielded the colubrid vertebra reported here are unconformably bounded below (kaolin) and above (Twiggs Clay sediments) by non-fossiliferous sediments (also see discussion in WESTGATE, 2001). Consequently, the Clinchfield sediments of the Hardie Mine are a locally discrete fossiliferous unit (local fauna) with no evidence of contamination by intrusive fossils from older or younger horizons. Additionally, the fossil reported here is not from an extant snake that became entombed in the fossiliferous matrix. It is well mineralized in the same manner and color as other fossils retrieved from the *in situ* sediments.
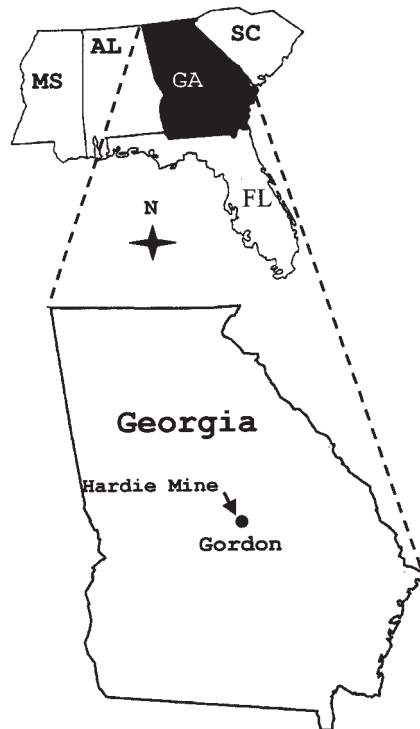

Fig. 1. General location of Hardie Mine fossil site in central Georgia, USA.

The Hardie Mine Clinchfield sediments were deposited during the Eocene events of the Jacksonian, but their age within the Eocene has been a matter of discussion. WESTGATE (2001) recently suggested that the sediments were deposited either during the late Middle Eocene (DOCKERY, 1996) or early in the Late Eocene (HUDDLESTUN and HETRICK, 1985; HUDDLESTUN, 1993). New faunal evidence, however, clearly points to a Late (but not latest) Eocene age for the fossil-bearing Clinchfield sediments of the mine. First, the shark fauna of the Hardie Mine is typical of other Late Eocene nearshore shark faunas of the Gulf Coastal region of North America (PARMLEY and CICIMURRI, ms in review). Additionally, a moderately large titanothere in the fauna (unstudied teeth in the Georgia College & State University Paleontological Collections) at least rules out an early Oligocene age as brontotherids were extinct by the end of the Eocene (MADER, 1998). The most compelling evidence for a Late Eocene age of the sediments, however, comes from invertebrate evidence. The pectinid species *Chlamys clinchfieldensis* STOCK is relatively common in the Hardie Mine molluscan fauna. GLAWE (1974) interpreted *C. clinchfieldensis* as being an excellent stratigraphic marker due to its widespread geographic distribution (central Georgia to western Alabama) and short stratigraphic range (Late Eocene only). Additionally, recent analysis of the Hardie Mine dinocysts by Lucy EDWARDS of the U.S. Geological Survey (written commun., 2001) suggests a Late Eocene age. The Hardie Mine dinocyst assemblage most closely resembles Georgia and South Carolina samples that have been placed in calcareous nannofossil Zone NP 19/20 (BYBELL et al., 1998; BYBELL, 2001; EDWARDS, 2001), which BERGGREN et al. (1995) have correlated to a Late Eocene age of 36.0-34.2 Ma.

II. SYSTEMATIC PALEONTOLOGY

The vertebral terminology and classification system used here follows HOLMAN (2000).

Class Reptilia: LAURENTI, 1768

Order Squamata OPPEL, 1811

Family Colubridae OPPEL, 1811

Subfamily Colubrinae OPPEL, 1811

Genus *Nebraskophis* HOLMAN, 1973

Nebraskophis sp. indet.

(Fig. 2)

M a t e r i a l. A middle trunk vertebra: Georgia College & State University Vertebrate Paleontological Collections (GCVP) 5217, collected from *in situ* matrix, Spring, 2001.

D e s c r i p t i o n a n d m e a s u r e m e n t s. In dorsal view, the vertebra is longer than wide. The posterior notch of the neural arch is broadly V-shaped. Only a small posterior section of the neural spine remains, but judging from it and the basal remnant of the spine, it was relatively thin and extended from the posterior edge of the zygosphenal roof to slightly past the
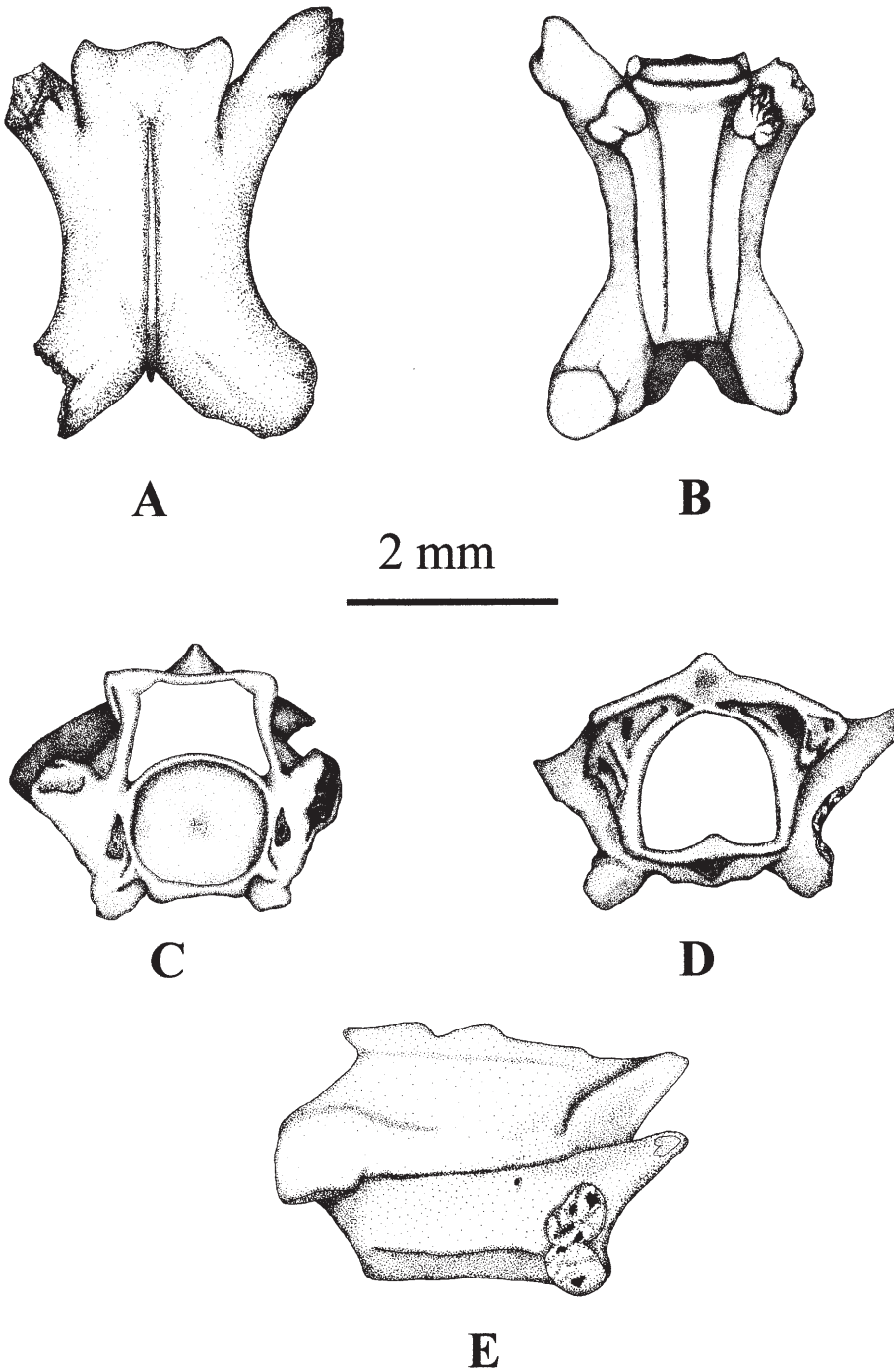
Fig. 2. Trunk vertebra (GCVP 5217) of *Nebraskophis* sp. from the Late Eocene Hardie Mine local fauna, Wilkinson County, Georgia, USA in dorsal (A), ventral (B), anterior (C), posterior (D), and lateral (E) views.

posterior notch of the neural arch. The distal part of the neural arch is missing on the left side, but a very weak epizygapophyseal spine is evident on the right side. The zygosphene is broad with the anterior edge trilobate. The left prezygapophyseal articular facet is missing, but the right facet is ovaloid.

In ventral view, the condyle is missing but the centrum is relatively narrow and gracile. The hemal keel is distinct, uniformly wide throughout its length with its surface broadly rounded rather than flat. A prezygapophyseal accessory process is present on the right side. The distal end is missing, but otherwise it is well developed and positioned obliquely to the long axis of the centrum. The paradiapophyses are damaged, but are distinctly divided into dorsal (diapophysis) and ventral (parapophysis) sections. The left postzygapophyseal articular facet is mostly missing, but the right facet is subtriangular.

In anterior view, the cotyle is round. Shallow depressions on either side of the cotyle each contain a well marked paracotylar foramen. The right prezygapophyseal articular facet is tilted dorsally. The zygosphene is thin and nearly flat dorsally.

In posterior view, the neural arch is moderately vaulted. A distinct foramen is present in each zygantral cavity. The left zygantral articular facet is missing, but the right facet is tilted upward.

In lateral view, the vertebra is longer than it is high. Because only a portion of the neural spine remains, its full height cannot be determined, but judging from the remaining part it was very low with its posterior border inclined. The interzygapophyseal ridge is distinct and thin. The subcentral ridge is worn, but it appears nearly straight and robust. The hemal keel is shallow, being only slightly produced off the floor of the centrum.

Measurements in millimeters of the fossil include: centrum length (estimated as the condyle is missing), 2.40; length through the left pre- and postzygapophyseal articular facets, 3.58; neural arch width measured at mid-section, 1.82; zygosphene width, 1.63.

T a x o n o m i c r e l a t i o n s h i p s. On the basis of characters given in HOLMAN (1981, 1984, 2000) and RAGE et al. (1992), the Hardie Mine snake vertebra is clearly assignable to the family Colubridae as follows: (1) vertebra lightly built in structure and elongated; (2) neural spine relatively long, thin, and reaches the roof of zygosphene; (3) prezygapophyseal accessory processes well developed; (4) zygosphene wide, thin anteriorly; (5) paradiapophyses distinctly divided into well-developed diapophyseal and parapophyseal components; (6) neural arch not posteriorly upswept; (7) paracotylar foramina present; (8) and hemal keel distinct with evident subcentral ridges. This combination of characters also distinguishes the vertebra from those of small boid, aniliid, and palaeopheid taxa known from the Eocene of North America.

On the basis of characters and discussion given in HOLMAN (1984, 2000) and WHISTLER and WRIGHT (1989) , the Hardie Mine colubrid best fits in the subfamily Colubrinae. It differs from North American Xenodontinae in having a higher neural arch and better developed hemal keel, and it lacks a hypapophysis that is characteristic of Natricinae trunk vertebrae.

In addition to *Nebraskophis*, two early Cenozoic colubrid genera are known from North America: *Texasophis* HOLMAN (early Oligocene to late Middle or early Late Miocene; HOLMAN, 2000) and *Floridaophis* HOLMAN (early Oligocene; HOLMAN, 1999). *Nebraskophis* and *Texasophis* are similar in having trunk vertebrae that are long and narrow in structural form with low neural spines (HOLMAN, 2000); the Hardie Mine vertebra is long and narrow in form and has a low neural spine. *Floridaophis* vertebrae are distinctly short and wide with comparatively high neural spines (HOLMAN, 1999), which easily separates the taxon from the former genera and the Hardie Mine fossil. A combination of characteristics distinguish the fossil from *Texasophis* to include: a longer and narrower vertebral morphology; a lower neural spine; stronger interzygapophyseal ridges; and a straighter and narrower hemal keel. It should also be mentioned that the fossil clearly differs from *Coluber cadurci* from the Early Oligocene of France (RAGE, 1974) in being more gracile overall with a narrower, more elongated centrum and wider hemal keel. HOLMAN (1999, 2000) has discussed in some detail the vertebral characters of *Nebraskophis*. The most diagnostic characters for

the genus are: (1) vertebral form elongated and narrow; (2) neural arch vaulted; (3) neural spine obsolete, posterior border slopes into neural arch; (4) hemal keel well-developed and distinct; and (5) interzygapophyseal ridges well developed. With one exception, the Hardie Mine fossil possesses these important features that characterize *Nebraskophis*. While the height of the neural spine in the fossil is well within the range seen in *Nebraskophis*, its posterior border does not slope into the neural arch, but instead it extends slightly past the posterior notch of the neural arch. The fossil probably represents a new species of the genus, but additional specimens are needed to confirm this.

III. DISCUSSION

Since the beginning of the Miocene (ca. 23.8 Ma), colubrids have diversified rapidly to become the most cosmopolitan and specious group of snakes today (e.g., Parmley and Holman, 1995; Holman, 1995, 2000), but very little is known about early (pre-Miocene) colubrids. Prior to the discovery of the Hardie Mine *Nebraskophis*, generically indeterminate colubrid vertebrae from the Late Eocene of peninsular Thailand (ca. 33.5-34.6 Ma; Benammi et al., 2001) represented the oldest known unquestionable fossils of the family Colubridae (Rage et al., 1992). Partially on the basis of these fossils, Asia is often cited as the probable continent from which colubrid snakes originated and spread to Western Europe and North America (e.g., Rage, 1982, 1987, 1988; Rage and Holman, 1984; Rage et al., 1992; Holman, 2000; Holman and Harrison, 2001). The Hardie Mine *Nebraskophis* is equivalent to, or slightly older in age than the Thailand colubrid by approximately 1.5-2 million years. Thus, colubrid snakes (at least of the subfamily Colubrinae) were present in North America by 36.0-34.2 million years ago. Given this, if the Asian continent was the center of origin for colubrid radiation and dispersal, then in order for at least some taxa to reach North America by 36.0-34.2 million years ago the origin of colubrids must considerably predate the Late Eocene. A pre-Late Eocene origin for colubrids now seems quite plausible considering that (1) non-Russellophiidae vertebrae strikingly similar to those of living Colubrinae snakes (identified as Colubroidea *incertae sedis*) are known from the Mid-Cretaceous of Sudan (Rage and Werner, 1999), (2) unquestionable Colubridae fossils appear at about the same time on the Asian and North American continents, and (3) these late Eocene colubrids already had vertebrae remarkably similar in build and structure to living Colubrinae snakes. Their vertebrae were, for example, elongated and lightly built with well developed neural spines, thin zygosphenes, divided paradiapophyses (not preserved on the Thailand vertebrae), paracotylar foramina, and distinct prezygapophysial processes.

Previous to the recent discovery of the small Colubrinae genera *Nebraskophis* and *Floridaophis* in the early Oligocene of Florida (Holman, 1999), early (pre-Miocene) colubrids were not definitively known from the southeastern region of North America. *Floridaophis* appears to have been a southeastern endemic while *Nebraskophis* was previously known from the Middle and Late Miocene of Nebraska (Holman, 2000). This (in part) prompted Holman and Harrison (2001) to suggest that an early Cenozoic biogeographic connection existed between the Great Plains and southeastern region of North America for at least some early colubrid snakes. The presence of *Nebraskophis* in the Late Eocene of Georgia clearly strengthens this argument for a Great Plains connection. Also, it is interesting to note that, to date, the oldest fossil finds of *Nebraskophis* have come from Late Eocene and Early Oligocene rocks of southeastern North America, not the Great Plains region. The genus does not show up on the Great Plains until about 17-18 million years later during the Middle Miocene (Medial Barstovian land mammal age; Holman, 2000). This, and given the fact that *Nebraskophis* is now known from the Late Eocene to the Late Miocene of North America (Holman, 1999, 2000) but is not known from the European or Asian continents suggest two things: *Nebraskophis* probably evolved autochthonously rather than arriving on the continent as a Eurasian immigrant; and the genus may have originated in the southeast and then dispersed westwardly to the Great Plains.

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